Applied Soil Ecology 129 (2018) 77–83

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Effect of water table decline on the abundances of soil mites, springtails, and nematodes in the Zoige peatland of eastern Tibetan Plateau

Xue Wei[a,b,c], Rui Cao[d], Xinwei Wu[d,*], Nico Eisenhauer[e,f], Shucun Sun[a,d]

[a] Center for Ecological Studies, Chengdu Institute of Biology, 9 Section 4 Renminnan Rd, Chengdu 610041, China
[b] College of Life Sciences, Sichuan University, 24 South Section 1 Yihuan Rd, Chengdu 610065, China
[c] University of Chinese Academy of Sciences, 19(A) Yuquan Rd, Shijingshan District, Beijing 100049, China
[d] Department of Ecology, College of Life Sciences, Nanjing University, 163 Xianlin Avenue, Nanjing 210023, China
[e] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany
[f] Institute of Biology, Leipzig University, Deutscher Platz 5e, 04103 Leipzig, Germany

ARTICLE INFO

Keywords:
Climate change
Human activities
Peatland
Qinghai-Tibetan Plateau
Soil fauna
Water table

ABSTRACT

Despite the important role of soil fauna in the decomposition of soil organic matter, the abundance response of soil fauna to environmental changes has been scarcely studied in peatlands, where soil carbon content is exceptionally high. The water table of the Zoige peatland, the largest alpine peatland worldwide, has been declining due to climate change and human drainage in recent decades, which likely induces changes in the abundance of soil fauna. In order to examine the abundance response of soil mites, springtails, and nematodes to water table decline in the Zoige peatland, we conducted an *in situ* field drainage experiment, consisting of low, intermediate, and ambient water table levels for four consecutive years. We measured the abundances of mites, springtails, and nematodes at five soil depths (0–5, 5–10, 10–15, 15–20, and 20–25 cm), for four times in the third and fourth year of the experiment. Results show that the effect of water table decline on the abundance of soil fauna varied among soil animal groups, soil depths, and the sampling times over the course of the experiment. While mites did not respond significantly to the experimental treatments, the abundance of springtails at soil depths of 0–5, 5–10, and 10–15 cm and that of nematodes at a depth of 15–20 cm were significantly higher in the drained treatments than in the undrained one. Moreover, water table decline increased the proportion of herbivorous nematodes in the top soil (0–5 cm) and decreased the proportion of bacterivorous nematodes at soil depths of 0–5 and 5–10 cm, while fungivorous and omnivorous-predaceous nematodes did not respond significantly. Given the demonstrated importance of soil fauna to soil carbon dynamics, the changes in the abundances of soil mites, springtails, and nematodes depicted here indicate that soil fauna should be further studied in relation to the recently reported rapid loss of soil carbon in the Zoige peatland.

1. Introduction

Anthropogenic environmental change is altering the composition and functioning of many ecosystems (Solomon et al., 2007), with peatlands representing one of the most vulnerable and functionally important ones in terms of carbon dynamics and feedbacks to the atmosphere (Sahagian and Melack, 1998). In particular, peatlands around the world are mostly experiencing water table decline (Kettridge et al., 2015), which may significantly decrease the soil carbon storage of peatlands. For example, low water table and associated increased oxygen availability (Straková et al., 2012) can directly enhance the decomposition rate of organic matter (Laiho, 2006). Moreover, it can also change the community composition of soil fauna and increase the abundance of soil fauna to indirectly accelerate the decomposition of soil organic matter in peatlands (Barreto and Lindo 2018; Laiho et al., 2001; Silvan et al., 2000; Vilkamaa, 1981). Thus, exploring the response of peatland soil fauna to water table decline is important to understand the mechanisms underlying peatland carbon dynamics.

Soil fauna has been widely demonstrated to be able to directly consume and fragment large particles of soil organic matter and enhance the diversity and biomass of soil microbes that are responsible for the decomposition of soil organic matter (Barreto and Lindo 2018; Kaneda and Kaneko, 2008; Laiho et al., 2001; Schmidt et al., 2016). However, in contrast to responses of plant communities and greenhouse gases fluxes (Cao et al., 2017a, b; Chimner and Cooper, 2003; Updegraff et al., 2001), the abundance response of soil fauna to water table

* Corresponding author.
E-mail address: wuxw@nju.edu.cn (X. Wu).

https://doi.org/10.1016/j.apsoil.2018.05.006
Received 23 January 2018; Received in revised form 8 May 2018; Accepted 8 May 2018
Available online 16 May 2018
0929-1393/ © 2018 Elsevier B.V. All rights reserved.

Table 1
Results of linear mixed models (LMMs) of the effects of water table (WT), sampling time and their interaction on the abundances of springtails, mites and nematodes, as well as the proportion of different groups of nematodes (herbivores, fungivores, bacterivores, omnivores-predators, and other nematodes) in each soil layer. Degree of freedom (DF) and Sum of squares (SS) values are provided. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Soil layer			Mites	Springtails	Nematodes	Relative proportion of different nematode groups				
						Herbivores	Fungivores	Bacterivores	Omnivores-predators	Other nematodes
		DF	SS	SS	SS	SS	SS	SS	SS	SS
0–5 cm	WT	2	0.98	3.69***	1696.46	26.25**	0.67	8.02*	6.42	0.43
	Date	3	2.62*	3.97***	14727.85***	22.88*	35.56***	2.17	1.14	7.85**
	WT*Date	6	0.34	1.24	1332.87	26.06	12.57	8.27	2.65	3.71
	Block	5	4.02**	5.70***	4383.17	19.17	2.2	8.01	7.14	1.26
	Error	55	12.38	9.93	29472.7	139.4	59.32	43.88	66.93	31.65
5–10 cm	WT	2	0.42	4.36***	293.08	22.18*	0.06	1.29	2.52	5.2
	Date	3	10.82***	3.28**	2984.78**	7.97	27.18***	5.6	1.86	26.00***
	WT*Date	6	0.15	0.32	663.61	9.26	11.62	8.36	2.42	3.28
	Block	5	1.66	2.54	2466.68*	5.98	6.83	13.57*	8.32	5.81
	Error	55	7.83	13.29	11023.7	140.56	69.07	56.87	64.45	66.16
10–15 cm	WT	2	0.26	3.32**	35.76	9.37	6.71	2.18	1.81	10.76
	Date	3	6.28***	4.42***	262.44**	43.01**	25.13*	9.2	19.96*	12.18**
	WT*Date	6	0.6	1.39	290.43*	7.43	14.4	13.45	3.25	7.02
	Block	5	0.44	1.82	19.88	27.76	19.57	11.64	11.84	12.6

decline has not been well studied in peatlands. Moreover, results of available peatland studies are idiosyncratic: some studies showed that water table decline increased the abundances and diversity of soil invertebrates in peatlands (Laiho et al., 2001; Silvan et al., 2000; Vilkamaa, 1981; Wasilewska, 1991, 2002, 2006), while some others revealed non-significant effects on the abundance of soil fauna (Krab et al., 2014). One possible explanation for this may be that these previous studies (e.g. Lv et al., 2014; Marx et al., 2016) mostly investigated and compared soil faunal communities between undrained peatlands and drained sites that had previously been peatlands, inducing potential confounding factors (e.g. difference in natural history between sites) that may obscure the interpretation of the effect of water table decline.

The Zoige peatland on the eastern Tibet Plateau, covering 4605 km^2 in area, is the largest alpine peatland in the world (Xiang et al., 2009). It stores 0.48 Pg of soil organic carbon (Chen et al., 2014), accounting for 6.2% and 1‰ of peat soil organic carbon storage in China and in the world, respectively (Cui et al., 2015). Like many other peatlands (Kettridge et al., 2015), the Zoige peatland is now experiencing unprecedented water table decline due to climate change and human activities. On the one hand, the temperature has increased by 0.4 °C per decade, and precipitation has decreased by 22 mm per decade over the past 40 years (Yang et al., 2014). On the other hand, the Zoige peatland has been largely drained for rangelands since the 1970s. Nearly 1000 artificial channels, with a total length of nearly 3000 km, have drained more than 40% of the total area of the Zoige peatland (Dong et al., 2010). These drainage channels must have increased water output from the Zoige peatland (Dong et al., 2010). Consequently, the water table has decreased from several cm to 85 cm below the surface in the Zoige peatland over the past several decades (Xiang et al., 2009). However, the abundance response of soil fauna to water table decline has never been studied in this peatland.

In this study, we explore the response of the abundance of the most dominant groups of soil meso- and microfauna (i.e., soil mites, springtails, and nematodes) to water table decline in the Zoige peatland by conducting an *in situ* field drainage experiment at a homogeneous site. Our experimental treatments are fully controlled and started from the same initial conditions before implementing the experimental treatments. Because the soil moisture of ambient peatlands is usually saturated and the experimental drainage increases soil aeration but does not lead to severe drought effects (Cao et al., 2017a; Wu et al., 2017), we hypothesize that water table decline increases the abundances of mites, springtails, and nematodes (although soil nematodes live in water films) in the Zoige peatland.

2. Materials and methods

2.1. Study site

This study was conducted in Hongyuan County (32°48′N, 102°33′E) of Sichuan Province in the Zoige peatland in the eastern Tibetan Plateau. The elevation is about 3500 m above sea level. The climate is a typical plateau continental zone climate with short-cool summer and long-cold winter. The annual mean temperature is 1.73 °C, with the maximum and minimum monthly means being 11.1 and −9.4 °C in July and January, respectively. The annual mean precipitation is 756 mm, 80% of which occurs between May and August (Cao et al., 2017a).

The Zoige peatland consists of lakes, wide river valleys, and marshy meadows (river terrace marshes), among which the area of marshy meadows is about 492 km^2, occupying 67.2% of the total peatland area (Lang et al., 1999). The peatland site where the study was conducted is mostly dominated by sedge species, including *Carex muliensis*, *Kobresia humilis*, *Scirpus pumilus*, *Blysmus sinocompressus*, *Kobresia setchwanensis* and *Kobresia pygmaea*. Rushes (*Juncus leucanthus* and *Juncus allioides*) are common but with relatively low abundance. Grasses, including *Poa pratensis*, *Deschampsia cespitosa* and *Agrostis matsumurae*, and forb species, including *Chamaesium paradoxum* and *Anemone trullifolia* var. *linearis*, are also abundant (Cao et al., 2017a). Total vegetation cover in midsummer is over 90%. The depth of peat layers in this region ranges from 0.3 to 10 m (Yang et al., 2014). The soil pH ranges between 6.6 and 7.0 (Yang et al., 2014), and the soil carbon and nitrogen concentrations range from 370 to 450 g kg^{-1} and from 13 to 19 g kg^{-1}, respectively, in the top 0–10 cm of the soil (Wu et al., 2017).

2.2. Experimental design and setup

We conducted a field experiment within a homogeneous peatland site to avoid possible confounding factors, such as variations in soil and vegetation conditions. The experiment was set up as a one-factor, three-level block design, with each block containing the ambient, intermediate, and low water table treatments. Each treatment was replicated six times, resulting in a total of 18 plots (Fig. S1).

The water table was manipulated by ditching in the homogeneous

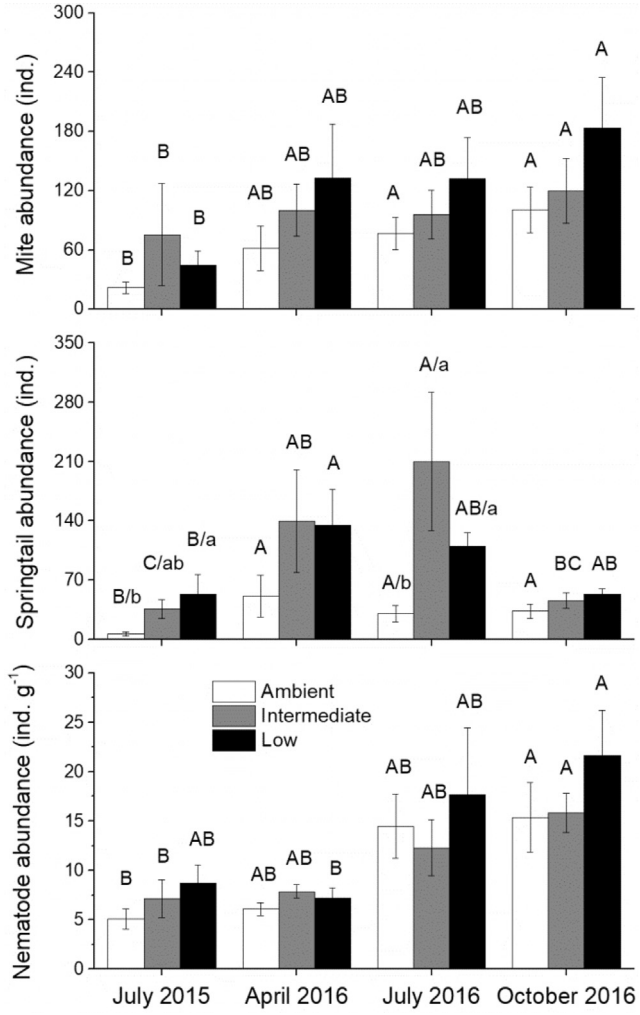

Fig. 1. Variations in the total abundances of mites, springtails and nematodes for the top soil (0–25 cm) as affected by ambient, intermediate, and low water table treatments. Different letters above the error bars denote statistically significant differences among treatments (lowercase) and sampling times (uppercase), respectively, as revealed by LMMs followed by *post hoc* Tukey's HSD tests for multiple comparisons. The differences among means are non-significant, if no letters are provided in each panel. Sample size was 6 for all treatments. Means ± standard error.

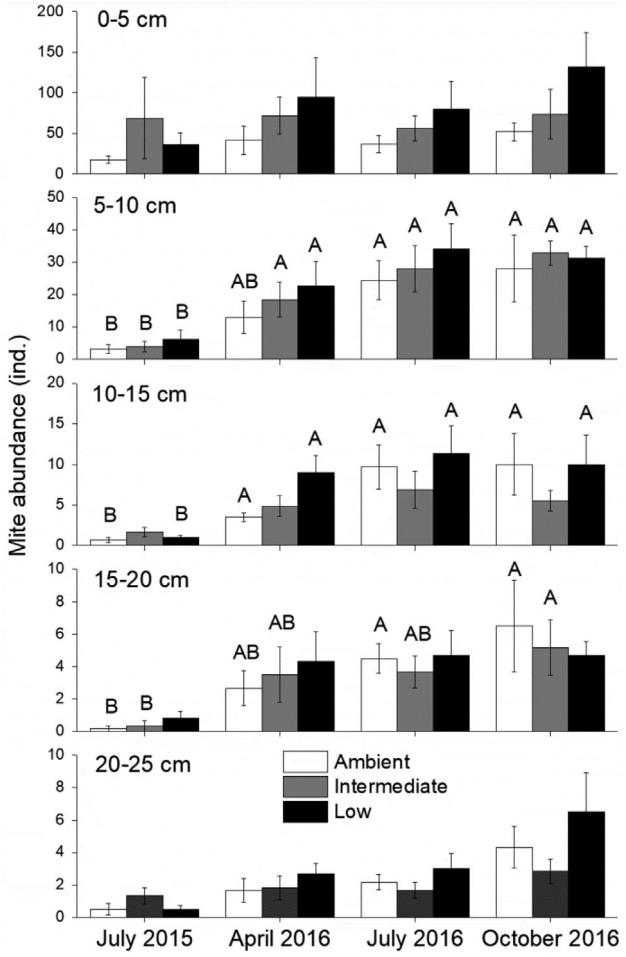

Fig. 2. Variations in the mite abundance for the soil depths of 0–5, 5–10, 10–15, 15–20, and 20–25 cm as affected by ambient, intermediate, and low water table treatments. Different letters above the error bars denote statistically significant differences among sampling times, respectively, as revealed by LMMs followed by *post hoc* Tukey's HSD tests for multiple comparisons. The differences between means are non-significant, if no letters are provided in each panel. Sample size was 6 for all the treatments. Means ± standard error.

peatland. In April of 2013, we dug a 240 m long, 0.5 m wide, and 1 m deep drainage ditch (called the major ditch thereafter) in a fenced, flat area of 150 × 150 m. The major ditch was connected to a small river. Eighteen 6 × 6 m quadrate plots were established (with regular intervals of 30 m between two adjacent plots) approximately 30 m away from the major ditch, with nine plots distributed along each side of the major ditch. Six plots were drained by 50 cm deep ditches, 6 plots by 20 cm deep ditches, and 6 plots were kept intact, which served as low, intermediate, and ambient water table treatments, respectively (Fig. S1).

Water table depth (the distance from the ground to the position of the water surface) was measured from one polyvinyl chloride (PVC) pipe (1.5 m in length and 5 cm in diameter, respectively) installed vertically in each plot using a 1.5 m long ruler every three to ten days during the experiment except for the freezing period (from November to March). The mean annual water table was about 11–22 cm and 9–16 cm lower in the low and intermediate treatments, respectively, than that in undrained plots during the experiment (Fig. S2). The average water table, which was calculated from the measurements during the experiment, was 58 cm and 51 cm in the low and intermediate treatments, respectively, lower than that in undrained plots (38 cm) during the experiment (Fig. S2). In addition, soil moisture (Water Scout SM100-6460-20) and temperature (Temp-3667-20) at 5 cm below the soil surface were also measured every 30 min over four years using data loggers (Watchdog 2000, Spectrum Technologies, Inc., USA). Average daily soil moisture was 10–21% and 4–14% lower in the low and intermediate treatments, respectively, than that in undrained plots, whereas there was no systematic difference in soil temperature (Fig. S3). The average soil moisture, which was calculated from the measurements during the experiment, was 28% and 32% lower in the low and intermediate treatments, respectively, lower than that in undrained plots (47%). The average soil temperature was indistinguishable among the low (13.6 °C) and intermediate (13.3 °C) treatments, and undrained plots (13.5 °C) during the experiment.

2.3. Field sampling and laboratory analyses

Soil samples were collected four times in the growing season (April to September), i.e. on 1 July of 2015, and 1 April, 1 July and 1 October of 2016 during the experiment. At each sampling date, two sets of soil samples (8 cm in diameter) were taken from depths of 0–5, 5–10, 10–15, 15–20, and 20–25 cm, respectively, at each plot. Samples were placed into paper bags and taken immediately to the laboratory. In the

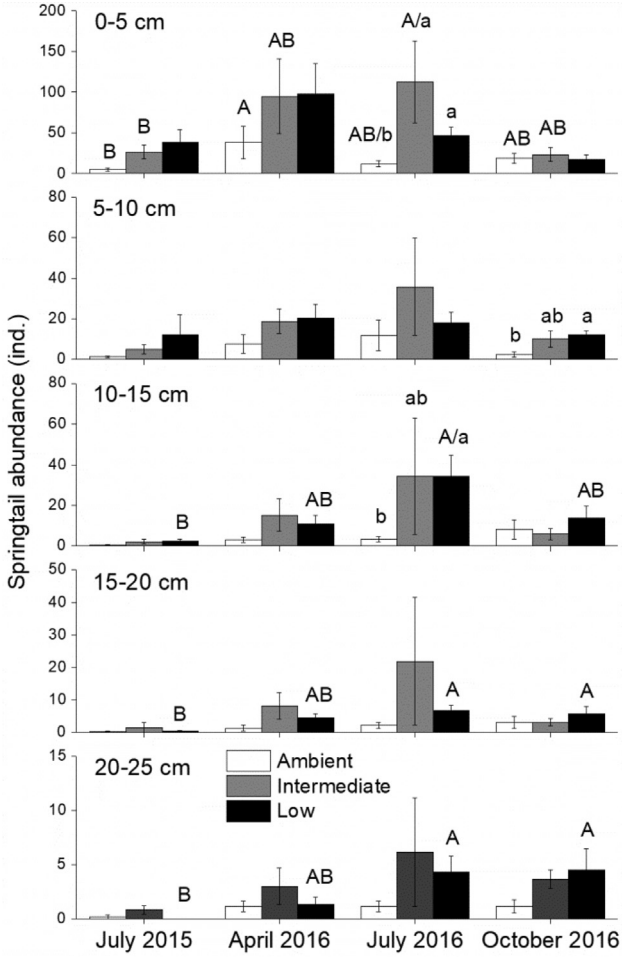

Fig. 3. Variations in the springtail abundance for the soil depths of 0–5, 5–10, 10–15, 15–20, and 20–25 cm soil layers as affected by ambient, intermediate, and low water table treatments. Different letters above the error bars denote statistically significant differences among treatments (lowercase) and sampling times (uppercase), respectively, as revealed by LMMs followed by *post hoc* Tukey's HSD tests for multiple comparisons. The differences between means are non-significant, if no letters are provided in each panel. Sample size was 6 for all the treatments. Means ± standard error.

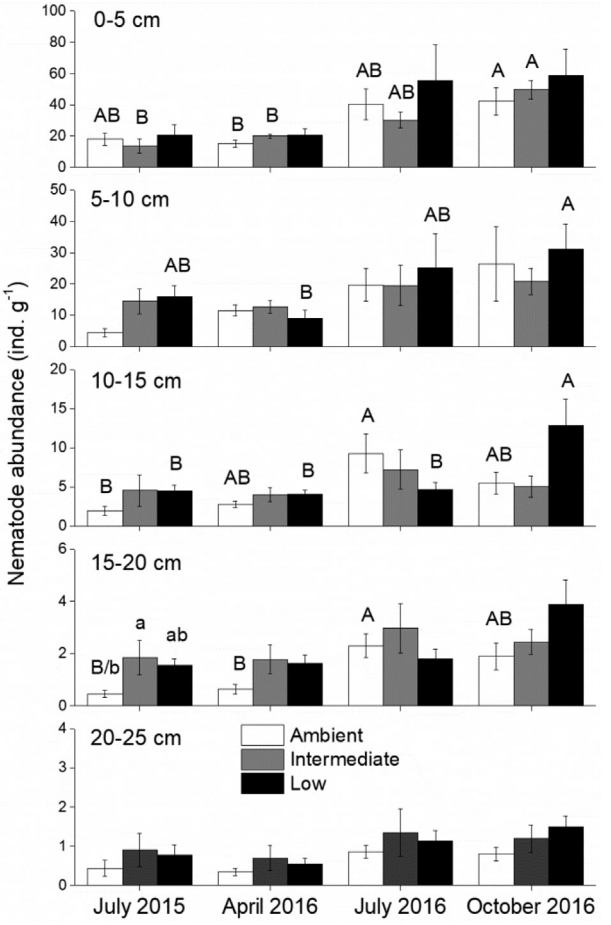

Fig. 4. Variations in the nematode abundance for the soil depths of 0–5, 5–10, 10–15, 15–20, and 20–25 cm soil layers as affected by ambient, intermediate, and low water table treatments. Different letters above the error bars denote statistically significant differences among treatments (lowercase) and sampling times (uppercase), respectively, as revealed by LMMs followed by *post hoc* Tukey's HSD tests for multiple comparisons. The differences between means are non-significant, if no letters are provided in each panel. Sample size was 6 for all the treatments. Means ± standard error.

laboratory, one set of soil samples was extracted using a high-gradient dry funnel extraction (Takeda, 1979). Of the microarthropods extracted from dry funnels, only mites and springtails were identified microscopically and counted. The abundances of mites and springtails were denoted as the number of mites and springtails collected from specific soil layers or whole soil cores. Besides that, 50 g of fresh soil from each of the other set of samples was extracted with Baermann funnels in a modified O'Connor wet extraction apparatus (Robinson and Heald, 1989). After wet extraction, nematodes were identified to the genus level and counted under a dissection microscope. The abundance of nematodes was denoted as the density of nematodes (per g dry soil) in each soil layer or in the whole soil core. Nematode community composition was assessed by assigning genera to trophic groups based on Yeates et al. (1993), allowing for an assessment of the abundances (number of individuals g^{-1} dry soil) of nematodes and the proportions of herbivores, bacterivores, fungivores, and omnivores-predators. All of the other species of nematodes, in addition to those four groups, were assigned to "other nematodes", and the proportion of the other nematodes was also calculated by dividing the abundance by total nematode abundance.

2.4. Data analyses

For each sampling time, we calculated the total abundances of springtails and mites by summing the abundances of springtails and mites from each soil layer per soil core, respectively, and averaged the abundance of nematodes from different soil layers as the average nematode abundance per g soil. Kolmogorov-Smirnov and Levene's tests were used to check for normality of the distribution and variance homogeneity of the sample residuals, respectively. The abundances of springtails and mites were log-transformed, and the proportion of different trophic groups of nematodes was square root transformed to achieve normality. The effects of water table, sampling date, and their interaction on the abundances of springtails, mites, and nematodes, as well as the proportions of different trophic groups of nematodes were determined using ANOVA with a linear mixed-effect model (LMM), in which water table and sampling date were set as fixed factors, block was included as a random factor. Once a significant factor effect was detected, *post hoc* Tukey's HSD tests were used to further determine the statistical differences among treatments and sampling dates, respectively, for each soil layer. In addition, we conducted correlation analyses (pooled data) to determine the correlative relationships among all the response variables. All the statistical analyses were conducted in R 3.3.1 (R Core Team, 2017).

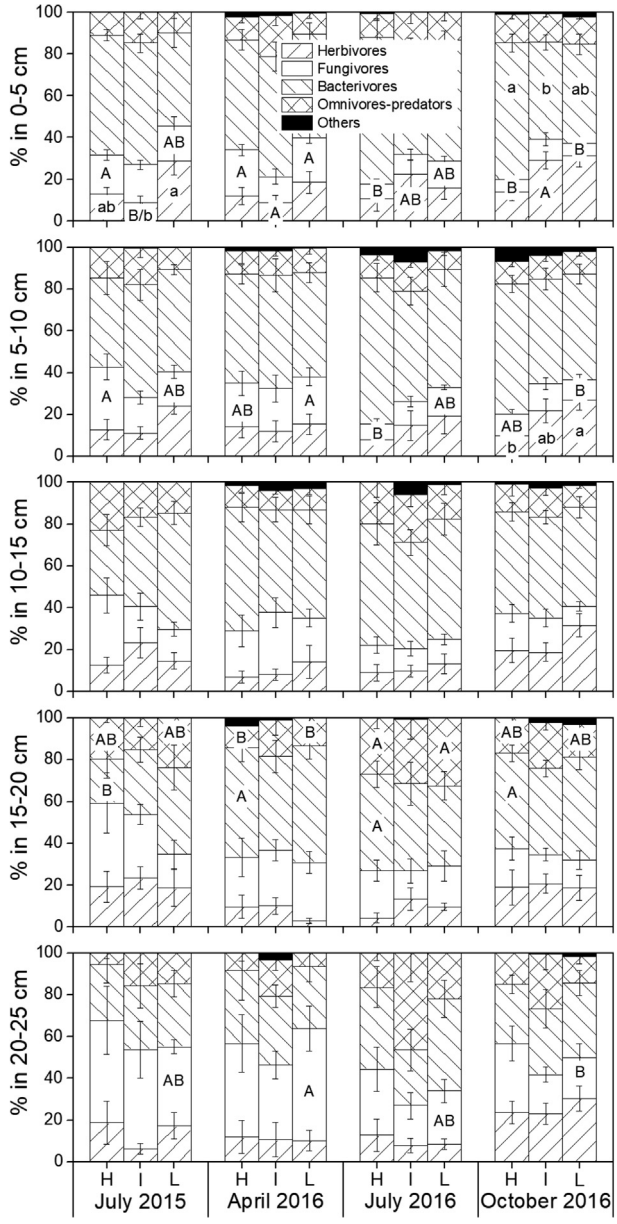

Fig. 5. The proportions of different nematode trophic groups (herbivores, bacterivores, fungivores, omnivores-predators, and other nematodes) for the soil depths of 0–5, 5–10, 10–15, 15–20, and 20–25 cm as affected by ambient, intermediate, and low water table treatments. Different letters above the error bars denote statistically significant differences among treatments (lowercase) and sampling times (uppercase), respectively, as revealed by LMMs followed by *post hoc* Tukey's HSD tests for multiple comparisons. The differences among means are non-significant, if no letters are provided in each panel. Sample size was 6 for all the treatments. Means ± standard error.

3. Results

3.1. Soil mites and springtails

Water table decline did not significantly change the total abundance of mites as well as mite abundance in each soil layer at all sampling times (Table 1; Figs. 1 and 2). However, mite abundance tended to increase with water table decline. Water table decline generally increased the total abundance of springtails, but this effect varied with sampling time and soil layer (Table 1; Figs. 1 and 3). Specifically, the total abundance of springtails was 726% and 264% higher in the low water table treatment than in the ambient water table treatment in July 2015 and 2016, respectively (Fig. 1). Moreover, for specific soil layers, the abundance of springtails was significantly higher in the low water table treatment than in the ambient water table treatment in soil depths of 0–5 cm (increased by 296% in July 2016), 5–10 cm (by 388% in October 2016), and 10–15 cm (by 939% in October 2016) (Fig. 3).

3.2. Soil nematodes

The average abundance of nematodes was higher, albeit this trend was not statistically significant, in the low and intermediate water table treatments than in the ambient water table treatment at all sampling times (Table 1; Fig. 1). Moreover, the effect of water table decline was non-significant for total nematode abundance in all soil layers and all sampling times except for that in 15–20 cm layer in July 2015, where the nematode abundance in the intermediate water table treatment significantly increased by 302% relative to that in the ambient water table treatment (Table 1; Fig. 4).

Water table decline generally increased the proportion of herbivorous nematodes, but the effect varied with soil depth and sampling time (Table 1; Fig. 5). Specifically, the proportion of herbivorous nematodes was higher in the low and intermediate water table treatments than in the ambient water table treatment at a soil depth of 0–5 cm in July 2015 and at a depth of 5–10 cm in October 2016 (Table 1; Fig. 5). Water table decline did not significantly affect the proportions of fungivorous nematodes, omnivorous-predaceous nematodes, as well as that of the other nematodes in all soil layers and sampling times (Table 1; Fig. 5). However, water table decline significantly decreased the proportion of bacterivorous nematodes at a soil depth of 0–5 cm in October 2016, but the water table effect was non-significant in the other cases (Table 1; Fig. 5).

3.3. Correlations among soil meso- and microfauna groups

Mite abundance was significantly positively correlated with springtail abundance ($r = 0.44$, $P < 0.001$) and nematode abundance ($r = 0.44$, $P < 0.001$), and a significant and positive correlation was also found between springtail abundance and nematode abundance ($r = 0.21$, $P < 0.05$).

4. Discussion

Water table decline in general enhanced the abundance of meso- and microfauna in the Zoige peatland, consistent with the results of earlier studies addressing the abundance response of soil fauna to drainage in many other peatlands (Laiho et al., 2001; Silvan et al., 2000; Wasilewska, 1991, 2002, 2006). Moreover, water table decline significantly increased the proportion of herbivorous nematodes and decreased the proportion of bacterivorous nematodes in the top soil, indicating shifts in the nematode community effects on ecosystem processes like plant growth and nutrient cycling. These results collectively suggest that the abundances, as well as community composition, of soil meso- and microfauna are sensitive to water table decline in the Zoige peatland.

The increase in the abundance of soil fauna is likely to result from the direct and indirect effects of water table decline. Firstly, water table decline changes the physical and chemical properties of the soil, such as soil moisture, temperature, and pH. For example, low temperature and high soil moisture are often postulated to be important limiting factors for soil fanua in cold climates (Hoschitz and Kaufmann, 2004). In the present study, albeit the indistinguishable difference in average soil temperature among treatments, the decline of soil moisture in the low and intermediate water table treatments might have enhanced soil porosity for gas diffusion and promote gas exchange, which should facilitate the population growth of soil fauna (Minkkinen et al., 2007). Moreover, water table decline likely changes the slightly acidic soil to alkalescent soil (Lv et al., 2014), and most species of soil mites,

springtails, and nematodes prefer to live in alkalescent soil conditions (Barnes et al., 2008), although we did not investigate soil pH in the present study. Secondly, water table decline might have indirectly increased the abundance of the soil fanua by changing the species composition and structure of the plant community. One of our previous studies that were conducted at the same experimental site demonstrated that water table decline increased abovegound plant biomass during our investigations, and increased the dominance of mesophyte species (grasses and forbs), while decreasing that of hygrophyte species (sedges and rushes) (Cao et al., 2017a). These changes likely lead to an increase in the biomass of both aboveground and belowground litter and the extension of plant roots to deeper soil layers, both of which might have contributed to the abundance increase of the soil fauna. In addition, the abundances of all taxa in the ambient plots were lower in July 2015 than in July 2016, which could be attributed to the greater inhibiting effect of high monthly mean soil moisture in July 2015 (51.8%) than in July 2016 (35.8%).

The changes in the relative abundance of nematode trophic groups can be due to both bottom-up and top-down effects induced by water table decline. On the one hand, possibly because of deeper and more intensive root growth, the proportion of herbivorous nematodes increased in the drained treatments, consistent with the results in several other peatlands (García-Palacios et al., 2013; Hansen and Coleman, 1998; Keith et al., 2009; Yeates, 1999). Similarly, decreased soil moisture due to water table decline often decreases the abundance of bacteria particularly at the upper soil layers (Jaatinen et al., 2007), which might be responsible for the decrease in the proportion of bacterivorous nematodes in the present study and also in other studies (e.g. Landesman et al., 2011). On the other hand, because many springtails and mites can directly feed on nematodes (Holtkamp et al., 2008; Kaneda and Kaneko, 2008; Koehler, 1999), a potential top-down effect of soil mites and springtails could affect nematode abundance. While the positive relationship among the three taxonomics groups rather suggest common drivers of population sizes and/or bottom-up effects, the decrease in the proportion of bacterivorous nematodes can also be partly due to the top-down control of mites and springtails that prefer to prey on bacterivorous nematodes (Kaneda and Kaneko, 2008). In addition, fungivorous nematodes are often less impacted by altered water tables (Landesman et al., 2011), such as also indicated by the present study, although fungi may benefit from water table decline (Jaatinen et al., 2007); the mechanism underlying this discrepancy is not clear.

Our results are generally consistent with the results of the studies investigating soil meso- and microfauna in peatlands or other types of wetlands. For example, the abundances of springtails and mites were about 100 times and 10 times higher in drained sites than those in undrained sites, respectively, in a pristine pine mire in southern Finland (Silvan et al., 2000). Moreover, consistent with our finding that springtails are more sensitive to drainage than mites, water table decline was found to affect the abundance of springtails but not mites when the water table was below 20 cm at the same study site (Laiho et al., 2001). Indeed, springtails are often more intolerant of wetness, preferring drier locations relative to mites (Laiho et al., 2001). Likewise, the abundances of soil mites and springtails were found to be higher in the natural peatland sites than in the reclaimed agricultural sites in the Sanjiang plain wetland in northeast China (Marx et al., 2016). In addition and also in line with our results, Wasilewska (1991, 2002, 2006) found that the abundances of nematodes and each of their trophic groups (i.e., herbivores, bacterivores, fungivores, omnivores and predators) were significantly higher in drained fens compared to natural fens, with the proportion of plant feeders being higher in drained fens than in natural fens.

In summary, by conducting a field experiment with fully controlled treatments, we demonstrated that water table decline may increase the abundances of soil mites, springtails, and nematodes. This confirms the results of long-term studies (decades), reporting chronic responses of soil meso- and microfauna to water table changes in peatlands (Laiho et al., 2001; Silvan et al., 2000). Considering the potential soil fauna-driven acceleration in organic matter decomposition and thus carbon release from peatland soils (Barreto and Lindo 2018; García-Palacios et al., 2013; Wu et al., 2017), we suggest that such soil faunal responses to water table decline should be incorporated into model predictions about peatland carbon storage under climate change. At a local and regional scale, we call for research addressing the effect of water table decline on soil fauna in the Zoige peatland.

Acknowledgements

We thank Kai He, Hanxiang Chen, Lei Hu, Dongbo Li and Bin Lan for their field assistance and Qinghai-Tibetan Research Base of Southwest University for Nationalities for providing research facilities. This study was supported by National Science Foundation of China [grant number 3150007 and 31470482] and the Fundamental Research Funds for the Central Universities. N.E. acknowledges funding by the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2018.05.006.

References

Barnes, N., Bamber, R.N., Moncrieff, C.B., Sheader, M., Ferrero, T.J., 2008. Meiofauna in closed coastal saline lagoons in the United Kingdom: structure and biodiversity of the nematode assemblage. Estuar. Coast. Shelf Sci. 79, 328–340. http://dx.doi.org/10.1016/j.ecss.2008.03.017.

Barreto, C., Lindo, Z., 2018. Drivers of decomposition and the detrital invertebrate community differ across a hummockhollow microtopology in Boreal peatlands. Ecoscience 25, 39–48. http://dx.doi.org/10.1080/11956860.2017.1412282.

Cao, R., Wei, X., Yang, Y., Xi, X., Wu, X., 2017a. The effect of water table decline on plant biomass and species composition in the Zoige peatland: A four-year in situ field experiment. Agr. Ecosyst. Environ. 247, 389–395. http://dx.doi.org/10.1016/j.agee.2017.07.008.

Cao, R., Xi, X., Yang, Y., Wei, X., Wu, X., Sun, S., 2017b. The effect of water table decline on soil CO_2 emission of Zoige peatland on eastern Tibetan Plateau: a four-year in situ experimental drainage. Appl. Soil Ecol. 120, 55–61. http://dx.doi.org/10.1016/j.apsoil.2017.07.036.

Chen, H., Yang, G., Peng, C., Zhang, Y., Zhu, D., Zhu, Q., Hu, J., Wang, M., Zhan, W., Zhu, E., Bai, Z., Li, W., Wu, N., Wang, Y., Gao, Y., Tian, J., Kang, X., Zhao, X., Wu, J., 2014. The carbon stock of alpine peatlands on the Qinghai-Tibetan Plateau during the Holocene and their future fate. Quat. Sci. Rev. 95, 151–158. http://dx.doi.org/10.1016/j.quascirev.2014.05.003.

Chimner, R.A., Cooper, D.J., 2003. Influence of water table levels on CO_2 emissions in a Colorado subalpine fen: an *in situ* microcosm study. Soil Biol. Biochem. 35, 345–351. http://dx.doi.org/10.1016/S0038-0717(02)00284-5.

Cui, M., Ma, A., Qi, H., Zhuang, X., Zhuang, G., Zhao, G., 2015. Warmer temperature accelerates methane emissions from the Zoige wetland on the Tibetan Plateau without changing methanogenic community composition. Sci. Rep. 5, 11616. http://dx.doi.org/10.1038/srep11616.

Dong, Z.B., Hu, G.Y., Yan, C.Z., Wang, W.L., Lu, J.F., 2010. Aeolian desertification and its causes in the Zoige Plateau of China's Qinghai-Tibetan Plateau. Environ. Earth Sci. 59, 1731–1740. http://dx.doi.org/10.1007/s12665-009-0155-9.

García-Palacios, P., Maestre, F.T., Kattge, J., Wall, D.H., 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecol. Lett. 16, 1045–1053. http://dx.doi.org/10.1111/ele.12179.

Hansen, R.A., Coleman, D.C., 1998. Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (Acari: Oribatida) in litterbags. Appl. Soil Ecol. 9, 17–23. http://dx.doi.org/10.1016/S0929-1393(98)00048-1.

Holtkamp, R., Kardol, P., van der Wal, A., Dekker, S.C., van der Putten, W.H., de Ruiter, P.C., 2008. Soil food web structure during ecosystem development after land abandonment. Appl. Soil Ecol. 39, 23–34. http://dx.doi.org/10.1016/j.apsoil.2007.11.002.

Hoschitz, M., Kaufmann, R., 2004. Soil nematode communities of Alpine summits–site differentiation and microclimatic influences. Pedobiologia 48, 313–320. http://dx.doi.org/10.1016/j.pedobi.2004.03.004.

Jaatinen, K., Fritze, H., Laine, J., Laiho, R., 2007. Effects of short- and long-term water-level drawdown on the populations and activity of aerobic decomposers in a boreal peatland. Glob. Change Biol. 13, 491–510. http://dx.doi.org/10.1111/j.1365-2486.2006.01312.x.

Kaneda, S., Kaneko, N., 2008. Collembolans feeding on soil affect carbon and nitrogen mineralization by their influence on microbial and nematode activities. Biol. Fert.

Soils 44, 435–442. http://dx.doi.org/10.1111/j.1740-0929.2008.00513.x.
Keith, A.M., Brooker, R.W., Osler, G.H.R., Chapman, S.J., Burslem, D.F.R.P., Wal, R.V.D., 2009. Strong impacts of belowground tree inputs on soil nematode trophic composition. Soil Biol. Biochem. 41, 1060–1065. http://dx.doi.org/10.1016/j.soilbio.2009.02.009.
Kettridge, N., Turetsky, M.R., Sherwood, J.H., Thompson, D.K., Miller, C.A., Benscoter, B.W., Flannigan, M.D., Wotton, B.M., Waddington, J.M., 2015. Moderate drop in water table increases peatland vulnerability to post-fire regime shift. Sci. Rep. 5, 8063. http://dx.doi.org/10.1038/srep08063.
Koehler, H.H., 1999. Predatory mites (Gamasina, Mesostigmata). Agris. Ecosyst. Environ. 74, 395–410. http://dx.doi.org/10.1016/S0167-8809(99)00045-6.
Krab, E.J., Aerts, R., Berg, M.P., van Hal, J., Keuper, F., 2014. Northern peatland Collembola communities unaffected by threesummers of simulated extreme precipitation. Appl. Soil Ecol. 79, 70–76. http://dx.doi.org/10.1016/j.apsoil.2014.03.007.
Laiho, R., 2006. Decomposition in peatlands: Reconciling seemingly contrasting results on the impacts of lowered water levels. Soil Biol. Biochem. 38, 2011–2024. http://dx.doi.org/10.1016/j.soilbio.2006.02.017.
Laiho, R., Silvan, N., Cárcamo, H., Vasander, H., 2001. Effects of water level and nutrients on spatial distribution of soil mesofauna in peatlands drained for forestry in Finland. Appl. Soil Ecol. 16, 1–9. http://dx.doi.org/10.1016/S0929-1393(00)00103-7.
Landesman, W.J., Treonis, A.M., Dighton, J., 2011. Effects of a one-year rainfall manipulation on soil nematode abundances and community composition. Pedobiologia 54, 87–91. http://dx.doi.org/10.1016/j.pedobi.2010.10.002.
Lang, H.Q., Zhao, K., Chen, K., 1999. Wetland Vegetation in China. Beijing Sci Press, Beijing, China.
Lv, Y., Gua, X., Zhang, W.D., 2014. The responses of soil nematode assemblages to disturbance in Liaohe estuary wetlands. Eur. J. Soil Biol. 61, 6–11. http://dx.doi.org/10.1016/j.ejsobi.2013.12.003.
Marx, M.T., Yan, X., Wang, X., Song, L., Wang, K., Zhang, B., Wu, D., 2016. Soil fauna abundance, feeding and decomposition in different reclaimed and natural sites in the Sanjiang Plain wetland, northeast China. Wetlands 36, 445–455. http://dx.doi.org/10.1007/s13157-016-0753-8.
Minkkinen, K., Lame, J., Shurpali, N.J., Mäkiranta, P., Alm, J., Penttilä, T., 2007. Heterotrophic soil respiration in forestry-drained peatlands. Boreal Environ. Res. 12, 115–126.
R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Found. Stat. Comput., Vienna Austria.
Robinson, A.F., Heald, C.M., 1989. Accelerated movement of nematodes from soil in baermann funnels with temperature gradients. J. Nematol. 21, 370–378.
Sahagian, D., Melack, J., 1998. Global Wetland Distribution and Functional Characterization: Trace Gases and the Hydrologic Cycle. IGBP Report 46.
Schmidt, A., John, K., Auge, H., Brandl, R., Horgan, F.G., Settele, J., Zaitsev, A.S., Wolters, V., Schädler, M., 2016. Compensatory mechanisms of litter decomposition under alternating moisture regimes in tropical rice fields. Appl. Soil Ecol. 107, 79–90. http://dx.doi.org/10.1016/j.apsoil.2016.05.014.
Silvan, N., Laiho, R., Vasander, H., 2000. Changes in mesofauna abundance in peat soils drained for forestry. Forest Ecol. Manage. 133, 127–133. http://dx.doi.org/10.1016/S0378-1127(99)00303-5.
Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L., 2007. Climate Change 2007: The Physical Science Basis Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, USA.
Straková, P., Penttilä, T., Laine, J., Laiho, R., 2012. Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: consequences for accumulation of organic matter in boreal peatlands. Glob. Change Biol. 18, 322–335. http://dx.doi.org/10.1111/j.1365-2486.2011.02503.x.
Takeda, H., 1979. On the extraction process and efficiency of MacFadyen's high gradient extractor. Pedobiologia 19, 106–112.
Updegraff, K., Bridgham, S.D., Pastor, J., Weishampel, P., Harth, C., 2001. Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. Ecol. Appl. 11, 311–326. http://dx.doi.org/10.1890/1051-0761(2001)011[0311:ROCACE]2.0.CO;2.
Vilkamaa, P., 1981. Soil fauna in a virgin and two drained dwarf shrub pine bogs. Suo 32, 20–122.
Wasilewska, L., 1991. The effect of moisture content of drained peat soils on soil nematode communities. Pol. Ecol. Studies 17, 191–201.
Wasilewska, L., 2002. Post-drainage secondary succession of soil nematodes on fen peat meadows in Biebrza Wetlands, Poland. Pol. J. Ecol. 50, 269–300.
Wasilewska, L., 2006. Changes in the structure of the soil nematode community over long-term secondary grassland succession in drained fen peat. Appl. Soil Ecol. 32, 165–179. http://dx.doi.org/10.1016/j.apsoil.2005.07.003.
Wu, X., Cao, R., Wei, X., Xi, X., Shi, P., Eisenhauer, N., Sun, S.C., 2017. Soil drainage facilitates earthworm invasion and subsequent carbon loss from peatland soil. J. Appl. Ecol. 54, 1291–1300. http://dx.doi.org/10.1111/1365-2664.12894.
Xiang, S., Guo, R., Wu, N., Sun, S., 2009. Current status and future prospects of Zoige Marsh in eastern Qinghai-Tibet Plateau. Ecol. Eng. 35, 553–562. http://dx.doi.org/10.1016/j.ecoleng.2008.02.016.
Yang, G., Chen, H., Wu, N., Tian, J., Peng, C., Zhu, Q., Zhu, D., He, Y., Zheng, Q., Zhang, C., 2014. Effects of soil warming, rainfall reduction and water table level on CH_4 emissions from the Zoige peatland in China. Soil Biol. Biochem. 78, 83–89. http://dx.doi.org/10.1016/j.soilbio.2014.07.013.
Yeates, G.W., 1999. Effects of plants on nematode community structure. Annu. Rev. Phytopathol. 37, 127–149. http://dx.doi.org/10.1146/annurev.phyto.37.1.127.
Yeates, G.W., Bongers, T., De Goede, R.G., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera-an outline for soil ecologists. J. Nematol. 25, 315–331.